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ANIMATIONS

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## 1. Introduction

Body mechanics and sensory feedback are central to the production of rectilinear peristaltic locomotion in the *Drosophila* larva [1; 2; 3; 4]. However, their importance for this animal's lateral motion and substrate exploration is unclear.

We present a model of planar larval mechanics coupled to a simple, reflexive nervous system. Our conservative mechanics produces axial compression waves and chaotic transverse bending. On addition of damping and driving forces, these motions are harnessed to produce forward and backward locomotion as well as deterministic chaotic exploratory behaviour. This is particularly surprising given that our neural model neither explicitly encodes nor controls the direction of movement (either forward/backward, or left/right).

## 2. Model construction

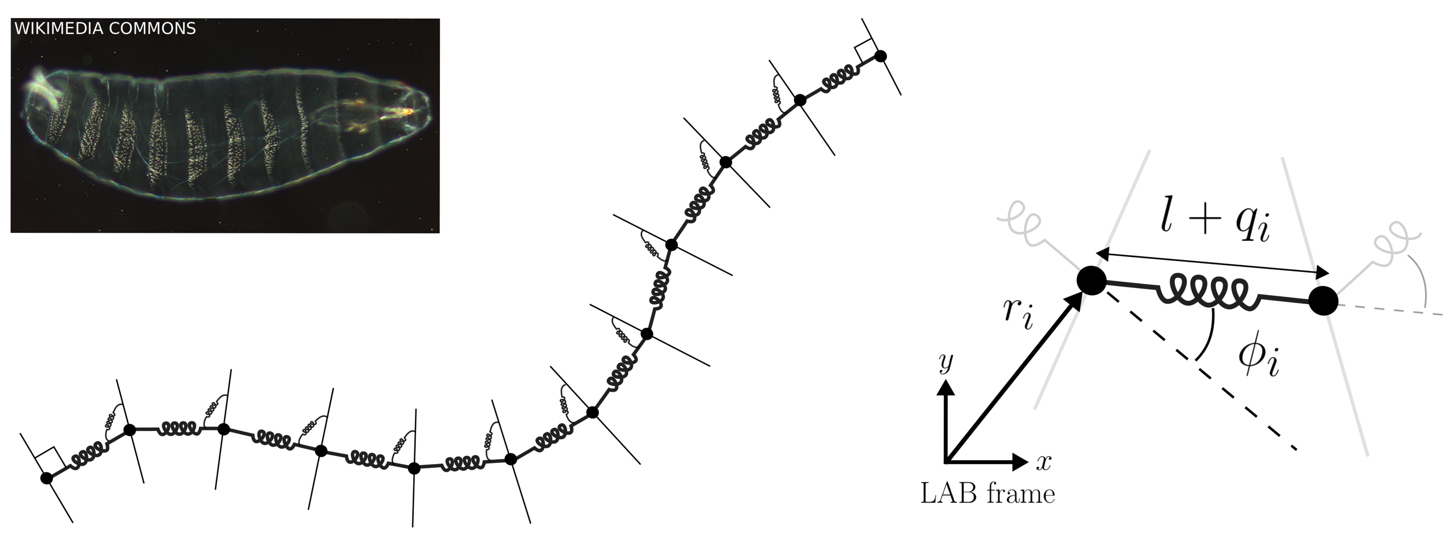


**Figure 1:** *a mechanical model of midline motion in the plane*

- The larval midline is modelled as a set of discrete point masses.
- Elastic energy is stored in axial compression/expansion and transverse bending.
- Energy is lost to viscous friction during motion.
- Masses interact with the substrate via Coulomb sliding friction.
- Head and tail are coupled via a total length constraint.

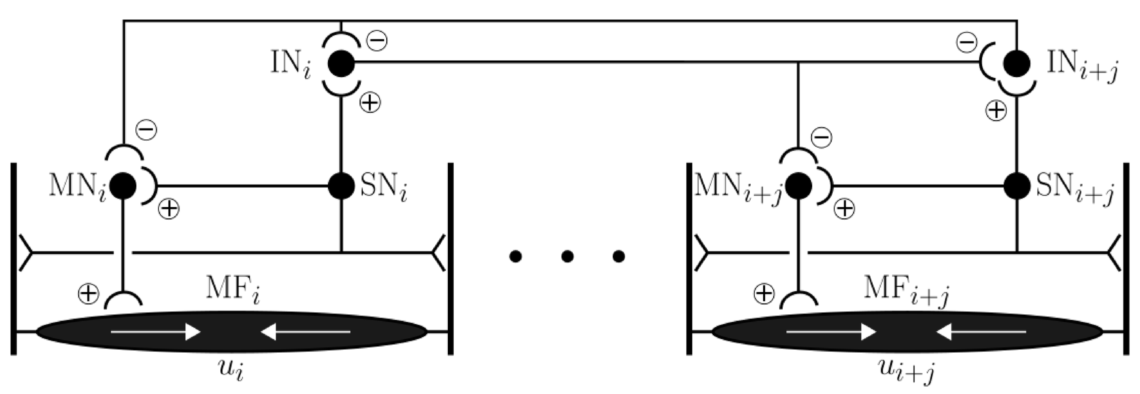


**Figure 2:** *segmental reflexes interacting via mutual inhibition*

- Neurons and muscles are binary (ON/OFF) and have no intrinsic dynamics.
- A reflex loop produces muscle tension within a segment when it is shortening.
- When a reflex is active, it inhibits distant neighbours.

## 3. Small-amplitude behaviour

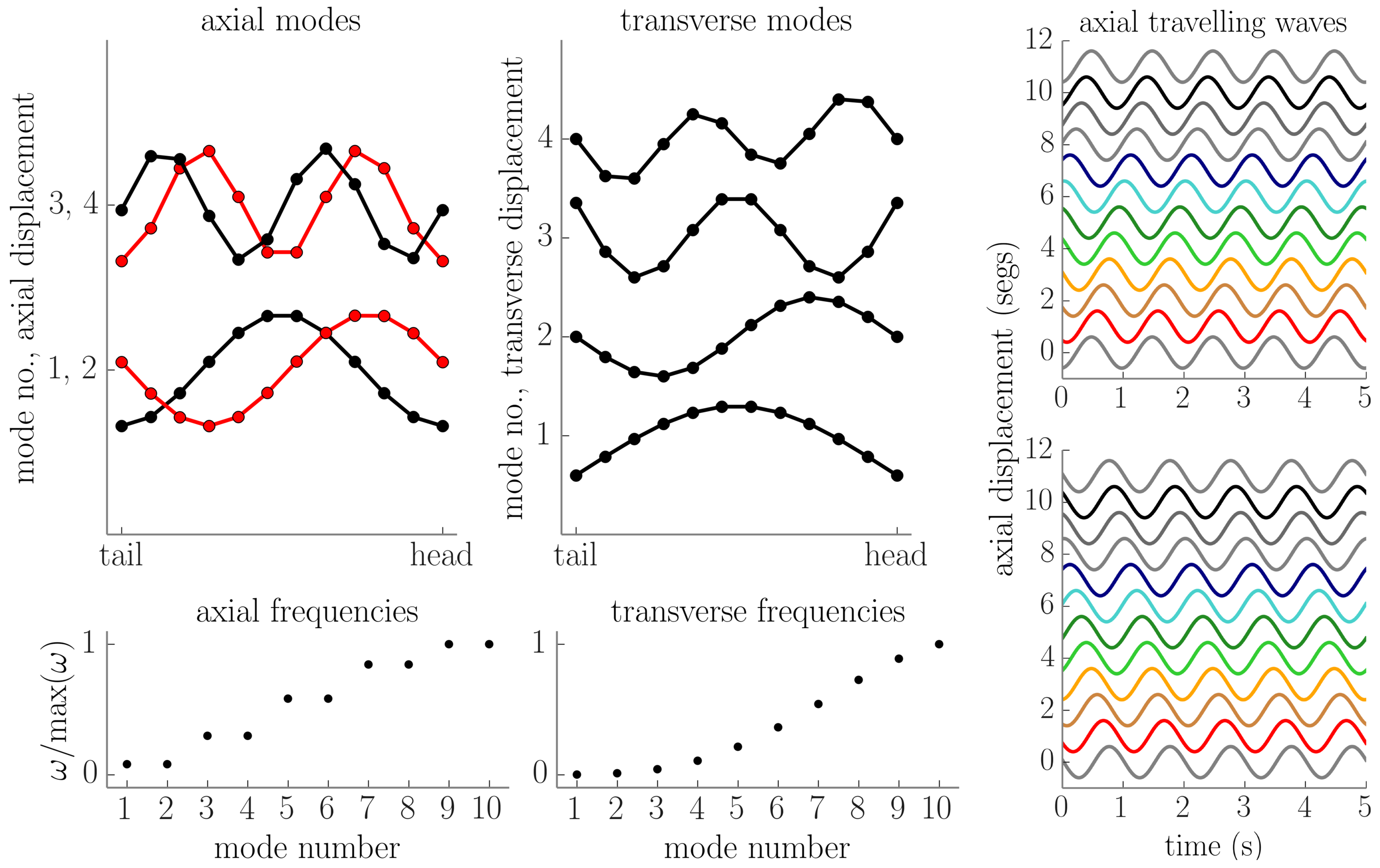


**Figure 3:** *modal analysis of conservative mechanics*

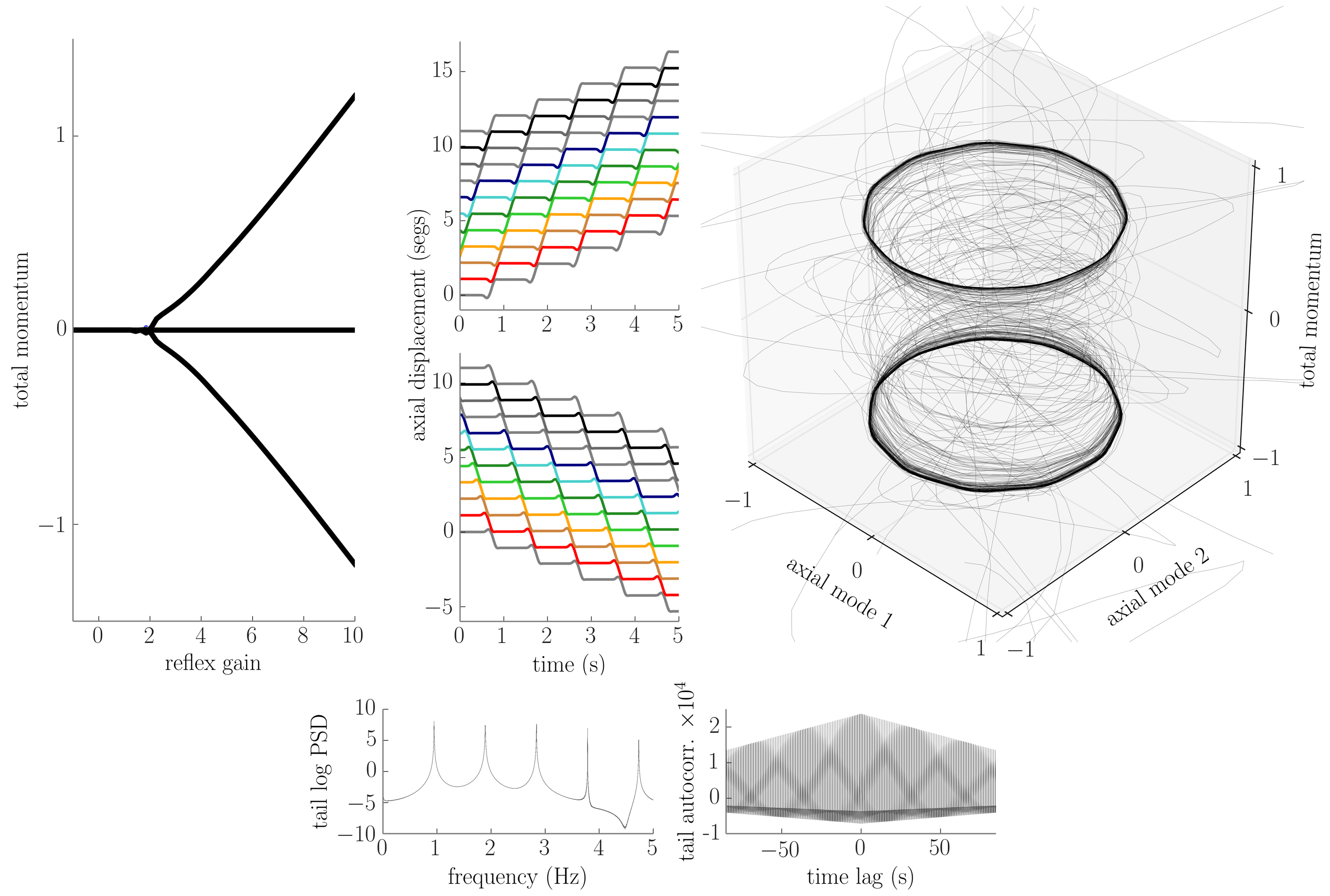


**Figure 4:** *emergence of limit cycles for forward and backward locomotion*

## 4. Large-amplitude behaviour

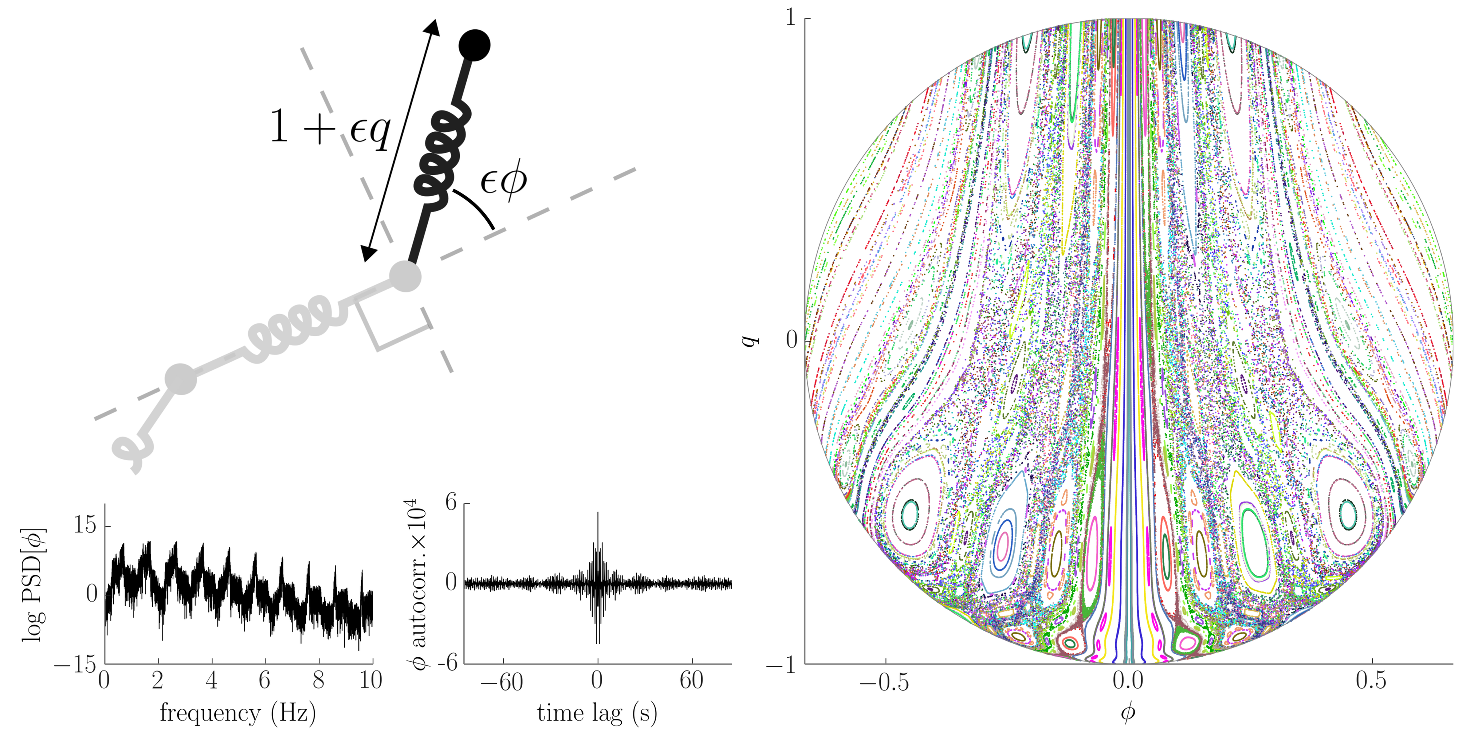


**Figure 5:** *conservative head motions become chaotic at large amplitudes*

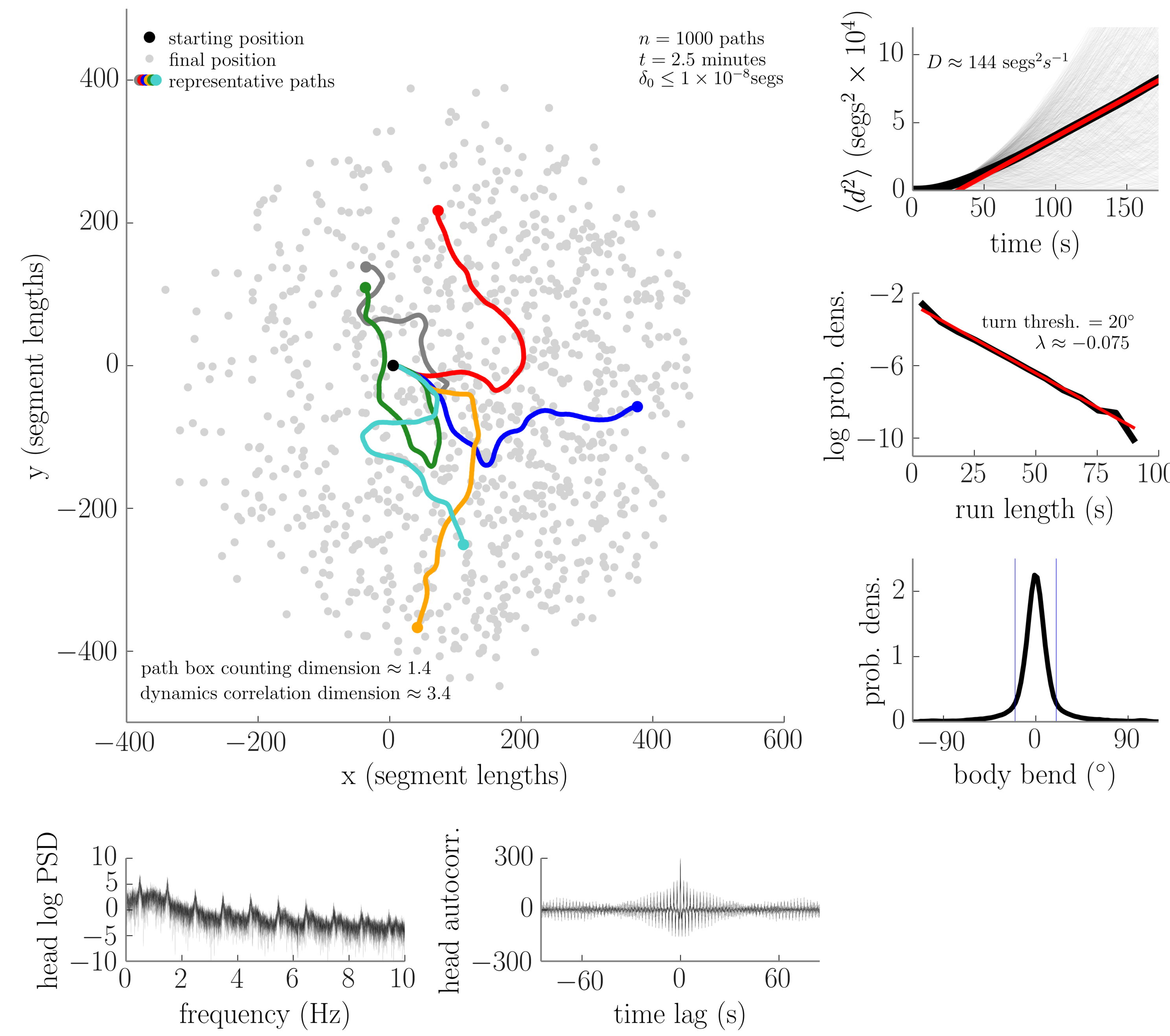


**Figure 6:** *deterministic chaotic exploration*

## 5. Conclusions

- Conservative body mechanics produces motions (axial travelling waves, chaotic transverse bending) suitable for substrate exploration.
- This allows stable forward and backward locomotion as well as turning/exploration to be generated by a single, simple reflex circuit.
- Intrinsic pattern generation and explicit encoding and control of the direction of travel are, in principle, unnecessary for successful exploration.

## References

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[4] Pehlevan, C., Paoletti, P., Mahadevan, L.: Integrative neuromechanics of crawling in *D. melanogaster* larvae. *eLife*, 5:e11031, (2016).